Changes in inbreeding of U.S. Herefords during the twentieth century¹

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ABSTRACT: Genetic diversity in the U.S. Hereford population was characterized by examining the level and rate of inbreeding and effective population size. Pedigree records for 20,624,418 animals were obtained from the American Hereford Association, of which 96.1% had both parents identified. Inbreeding coefficients were computed and mean inbreeding $(F_{\bar{x}})$ calculated by year from 1900 to 2001. Inbreeding increased rapidly between 1900 and 1945. From 1946, inbreeding increased linearly to a maximum of 11.5% in 1966. Throughout the 1970s and 1980s, mean inbreeding decreased to mid-century levels. Several alternatives were investigated to explain this decline. The average relationship between prominent sires fell from 20 to 12% during the time that the level of inbreeding decreased, which reflects an increase in the popularity of certain less fashionable sire lines that would have temporarily decreased inbreeding. Pedigrees were constructed for animals born after 1990. This subsample of animals with no missing ancestors in at least 12 generations did not exhibit a decrease in inbreeding.

Missing ancestral information therefore contributed to the apparent decline. One cause of missing ancestry results from outcrossing to imported animals. The effect of missing ancestry was investigated by simulating the missing ancestors. In 2001, Fx was 9.8%, and approximately 95% of individuals were inbred. The maximal inbreeding coefficient was 76%. The annual change in mean inbreeding $(\Delta F_{\bar{x}})$ was estimated for Herefords born during five time periods from 1946 to 2001, where inbreeding was changing at different linear rates. The $\varDelta F_{\bar{x}}$ for the most recent generation (1990 to 2001) was 0.12%/yr. Assuming a generation interval of 4.88 yr, the estimated effective population size was 85. This study provides a benchmark of current genetic diversity in the Hereford population. Results indicate that inbreeding is accumulating linearly and below critical levels. Increases in the adoption of reproductive technologies could decrease genetic diversity, and in the future, we may need to consider strategies to minimize inbreeding.

Key Words: Hereford Cattle, Inbreeding, Effective Population Size, Genetic Diversity

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Introduction

The adoption of technologies that facilitate widespread dissemination of animal germplasm over the past century have likely affected genetic diversity in cattle populations. Researchers have evaluated genetic relationships and genetic variation within breeds of dairy cattle, but few breed-wide analyses are available for U.S. beef cattle. The objectives of this research were to 1) characterize genetic diversity in the U.S. Hereford population by examining the level and rate of inbreeding and effective population size; 2) explore the reasons

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for changes in inbreeding levels; and 3) have available baseline information for evaluating strategies to maintain genetic diversity.

Herefords were imported into the United States from England in the mid-19th century. Prominent lines emerged and gained in popularity, increasing the likelihood of related mates and potentially decreasing genetic variation in the population. No comprehensive analysis of the Hereford pedigree has been performed, but several researchers have evaluated genetic diversity in Hereford subpopulations (Burrow, 1993). Willham (1937) sampled popular lines from the entire breed in 1930 and calculated a mean inbreeding coefficient of 8.1%. Stonaker (1951) reported inbreeding of 30.7% for a closed herd in 1947, and Russell et al. (1984) reported inbreeding of 37.0% for another closed line in 1984. Blott et al. (1998) subsampled Herefords from Canada and the United Kingdom and found significant genetic differences between countries; Canadian Herefords

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Table 1. Structure of the Hereford pedigree

Item	No. of animals	% of total
Animals in pedigree	20,624,418	100
Sires	837,215	4.1
Dams	5,866,055	28.4
One parent unknown	690,974	3.4
Both parents unknown	111,992	0.5
Both parents known	19,821,452	96.1

were more homozygous than cattle in other countries, and have almost completely displaced British Hereford genetics in a significant proportion of the British Hereford population. Such global and national dynamics make the Hereford an interesting case study for evaluating genetic diversity.

Materials and Methods

Description of Data

Pedigree records (n = 20,624,418) were obtained from the American Hereford Association (Kansas City, MO), which maintains records on all U.S. registered Hereford cattle. The records for this study contained animal, sire and dam identification, sex, and dates of birth ranging from 1900 to 2001, representing more than 20 generations. The number of records from 1900 to 1945 was limited because not all animals in the herd book had been entered into the Association's electronic pedigree file.

Analysis Procedures

The pedigree was checked to ensure integrity of the data and records were ordered so that parents appeared before their offspring, using the Animal Breeder's Tool-Kit (ABTK; Golden et al., 1992). Data edits were performed to rectify issues such as individuals listed as both sire and dam or offspring with dates of birth before those of their parents. Data edits resulted in a total of 6,093 sire and dam observations being removed from individuals' records. In the resulting pedigree records, over 96% of individuals had two known parents (Table 1).

Inbreeding Levels. Inbreeding coefficients $(\mathbf{F_x})$ were calculated using the ABTK based on the algorithm described by Meuwissen and Luo (1992). The computing time required to calculate inbreeding was approximately 4.5 d on a Pentium III, dual 1.4-GHz processor with 2 GB of RAM. Mean inbreeding $(\mathbf{F_x})$ and the proportion of inbred cattle were calculated for each birth year from 1900 to 2001 using all data. This should not be interpreted as implying 1900 was the base year for inbreeding, as some pedigrees extend to earlier time frames. The base is therefore before 1900 but of undetermined year. A total of 1,108,162 animals were excluded from further analysis due to missing date of

birth, yielding 19,516,256 animals or 94.6% of the pedigree records.

1990 to 2001 Population Subset. A subset of the population (n = 1,656,153) born between 1990 and 2001 was of special interest because they were more likely to be influential in contributing genes to the current population. The completeness of the pedigree for three generations before animals born in this time period is shown in Figure 1. More than 95% of individuals in this subset had known parentage in the second generation and very little information was lost in the two previous generations. By the sixth generation, over 91% of the pedigrees had no missing ancestors (results not shown).

Changes in Inbreeding. Three different approaches were used to study changes in the inbreeding trend from 1950 to 2001. Inbreeding changes in the first half of the century were affected by incomplete pedigree recording and thus were not considered for further analysis. The first approach was to evaluate the genetic relationships between prominent sires and sire ancestry. Coefficients of relationship between the top 25 progeny-producing sires each year from 1950 to 2001 were calculated based on the algorithm of Quaas (1976). Sire pedigrees also were analyzed for the same time period, and the percentage of sires with unknown parentage was identified. Changes in relationships and the number of sires with unknown parentage were evaluated relative to the inbreeding trend.

The second approach used to examine inbreeding trend was to develop a subsample of animals born from 1990 to 2001 that had all ancestors known for at least 12 generations. Mean inbreeding by birth year was computed for that subsample of animals and all their ancestors, comprising approximately 401,764 animals. This sample represented the Hereford population as it would have been with no animal importations and no missing pedigree information (subsequent to 1950).

The third approach for evaluating the inbreeding trend was to simulate the effect of imported sires and dams on the population. Three scenarios were simulated using a three-generation pedigree of animals (n = 1,656,153) born between 1990 and 2001: **REP0** = a control where 5% of individuals had unknown parentage; **REP1** = all animals with unknown parentage were assumed to have the same single sire and single dam, which were unrelated to the rest of the population; and **REP10** = all animals with unknown parentage were assumed to have one of 10 sires and 10 dams that were unrelated to the rest of the population. Scenarios REP1 and REP10 represent worst-case situations, where all imported animals are related through few parents. Mean inbreeding for each year from 1950 to 2001 was computed for each scenario and the trends were compared.

Annual Change in Inbreeding and Effective Population Size. Inspection of the trend relating inbreeding level to birth year identified five periods with apparent different linear rates of accumulation. These periods were 1946 to 1966; 1967 to 1969; 1970 to 1979; 1980 to 1989;

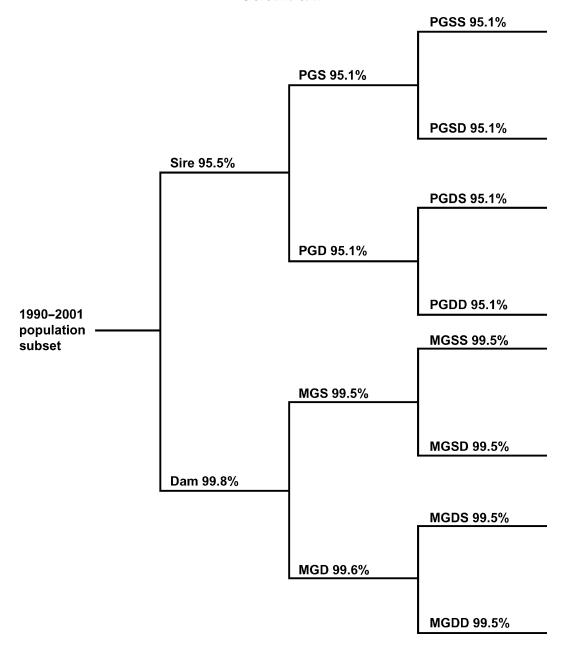


Figure 1. Percentage of known ancestors for animals born between 1990 and 2001. Each value refers to a percentage of the 1990 to 2001 population subset. PGS = paternal grand sire, PGD = paternal grand dam, MGS = maternal grand sire, MGD = maternal grand dam, PGSS = paternal grand sire's sire, PGSD = paternal grand sire's dam, PGDS = paternal grand dam's sire, PGDD = paternal grand dam's dam, MGSS = maternal grand sire's sire, MGSD = maternal grand sire's dam, MGDS = maternal grand dam's dam.

and 1990 to 2001. The annual change in mean inbreeding ($\Delta F_{\bar{x}}$) was calculated separately for each period as the regression of individual inbreeding on birth year. Pairwise comparisons of the rates of inbreeding in these five periods were undertaken using F-tests.

The effective population size of the breed was estimated using the rate of inbreeding:

$$N_e = \frac{1}{2 \varDelta F_{x \cdot L}}$$

where $\Delta F_{x\cdot L}$ is the change in inbreeding per generation (Falconer and Mackay, 1996), computed from ΔF_x (per

year) in product with the generation interval (L) computed as the average age of the parents of animals born between 1990 and 2001.

Results and Discussion

Inbreeding Levels

The time frame and number of animals included in the study provides an opportunity to examine how genetic relationships of a purebred cattle population change, not only over time, but as different economic traits were emphasized in the cattle industry. Table 2

Table 2. Inbreeding calculated for the Hereford pedigree for birth years 1900 to 2001

Inbreeding characteristic ^a	% F ^b
F_{xMIN}	0.0
F_{xMAX}	76.0
F_{xMIN}	0.9
F_{xMAX}	11.5
F_{x2001}	9.8

 $^{^{}a}F_{xMIN}$ = minimum individual inbreeding; F_{xMAX} = maximum individual inbreeding; F_{xMIN} = minimum mean inbreeding; F_{xMAX} = maximum mean inbreeding; F_{x2001} = mean inbreeding in 2001.

Assumes an unknown base year before 1900.

provides ranges of individual and average inbreeding levels from 1900 to 2001. Over the 102 yr of Hereford pedigree data, the minimum $F_{\bar{x}}$ was estimated as 0.9% in 1903, increasing to a maximum of 11.5% in 1966 (Table 2). The maximum inbreeding coefficient was 76% for a cow born in 1999, exceeding the maximum value of 68% reported by Russell et al. (1984) for a line of Herefords intensively inbred for approximately 30 yr. Such extreme inbreeding could be expected in the Herefords, where by 1999, the majority of animals have some degree of inbreeding, and where many closed lines have been formed. A longitudinal evaluation of mean inbreeding $(F_{\bar{x}})$ and number of animals by birth year are shown in Figure 2. For the first 30 yr of available data, $F_{\bar{x}}$ increased at a slow rate $(\Delta F_{\bar{x}}) = 0.0005$) and then accelerated before a rapid increase in the number of animals with known dates of birth. There were small numbers of Herefords in the pedigree file from 1900 to 1945 (averaging just under 400/yr), but in 1946, there were more records (28,569) than for all previous years combined and more than 10 times the records of the preceding year. These numbers do not reflect actual registrations before 1946; rather, they represent the sample of the population that had been entered into the database. The difference between pre- and post-1946 numbers in this study is due in part to the large number of records (1,108,087) initially used in calculating inbreeding but excluded from further analysis due to missing birth dates, as many of these excluded animals appear at the beginning of the pedigree. The number of records reached its maximum in 1952, and by the 1980s and 1990s, there were substantial decreases compared with mid-century numbers.

The $F_{\bar{x}}$ increased from 1930 to 1966, when it reached a peak and remained virtually unchanged until 1970, when a decrease began. By 1985, inbreeding had fallen to 8.9%, which was equivalent to inbreeding levels in the early 1950s. The decrease in mean inbreeding occurred in conjunction with a 55% decrease in animal numbers from 1960 to 1985. The negative inbreeding trend, after a period of steady increase, is unusual and dissimilar to trends reported for other breeds (Wiggans and VanRaden, 1995; Gutierrez et al., 2003), with the exception of Kearney et al. (2004), who reported a slight decrease (<0.5%) in inbreeding that was attributed to outcrossing with imported sires. Subsequent to the 1985-to-1992 plateau, $F_{\bar{x}}$ increased from 9.2% in 1993 to 10.2% in 2000. Mean inbreeding in 2001 was 9.8%.

Figure 3 illustrates the rapid increase in the proportion of inbred animals, especially leading up to 1945. The proportion of inbred animals decreased sharply in 1946 and 1947 before increasing in the 1950s. This abrupt change was probably artificial and could have been due to the increase in the number of complete

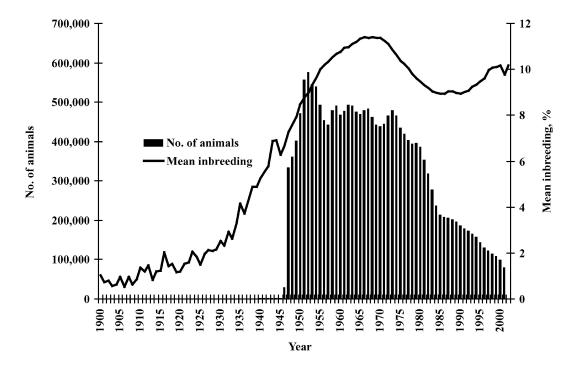


Figure 2. Mean inbreeding and number of Herefords (with known birth year) from 1900 to 2001.

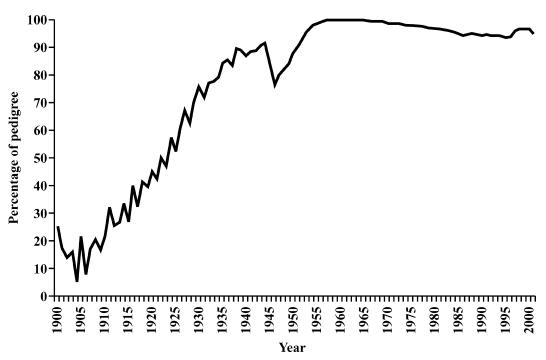


Figure 3. Percentage of pedigree with an inbreeding coefficient greater than 0.5% for birth years 1900 to 2001.

records in 1946 compared with the previous years. By 2001, nearly 95% of individuals were inbred. Though cases of extreme inbreeding were rare (<0.05% had an $F_{\rm x}>50\%$), it is clear that some producers, particularly those perpetuating closed lines, have mated highly related individuals. Although most Herefords have some level of inbreeding, the $F_{\rm x}$ of 9.8% suggests few consanguineous matings.

The inbreeding estimates from 1900 to 1930 do not agree with the findings of Willham (1937) based on the 1860 to 1930 Hereford population. Willham (1937) sampled randomly from the Hereford herd book for each year and traced the individual pedigrees back to ancestors born before 1860. Willham (1937) found an average inbreeding coefficient of 2.7% in 1900 and 8.1% in 1930, with an annual increase of 0.68% up to 1920, and 2.5% from 1920 to 1930. Continuation of such an increase from 1930 would have resulted in a much larger $F_{\bar{x}}$ in 2001 than 9.8%, and certainly the breed would be encountering inbreeding depression. In the current study, the $F_{\bar{x}}$ in 1930 was 2.5%, and the number of animals in the pedigree for that year (312), while smaller than the actual number of registrations (101,000; Anderson, 1932), was similar in size to the Willham (1937) sample. These 312 animals may not be representative of the entire population; thus, the inbreeding coefficient of 2.5% is probably not representative of the Hereford population at that time. However, these animals are highly relevant to current levels of inbreeding as these are ancestors of current animals.

The $F_{\bar{x}}$ of 9.8% in 2001 is considerably larger than those recently reported for other cattle populations. An average inbreeding coefficient of 1.0% was found in U.S.

Limousin (Gengler et al., 1998), 5% in Japanese Black cattle (Nomura, et al., 2001), less than 5% in the major U.S. dairy breeds (Wiggans et al., 1995), and less than 3% in U.K. Holsteins (Kearney et al., 2004). The inbreeding in these studies is related to a fairly recent base year (most using 1960); the present study used all animals in the pedigree dating back to 1900 and related inbreeding to an older foundation population. Young and Seykora (1996) found that estimates of inbreeding were considerably decreased when using more recent base years, but that the rate of annual increase was virtually unchanged, suggesting that although the estimated $F_{\bar{x}}$ by year provides a useful illustration of changes in the genetic structure of the Hereford population over time, it is the annual change in inbreeding that is most useful in comparing populations.

Population Subset 1990 to 2001

The long-term inbreeding trend demonstrates how inbreeding accumulated in the Hereford population over time; however, cattle born between 1990 and 2001 will yield the greatest insight into $F_{\bar{x}}$ in future generations. Figure 2 shows an increase in mean inbreeding after 1990 that, even with the drop in 2001, suggests increased homozygosity in Herefords. Potential factors contributing to lost genetic diversity include the 50% decrease in the number of animals in the pedigree during the 11-yr period or increased selection intensity (Weigel, 2001). Although selection intensity was not determined, it seems likely that technological improvements, such as AI, will lead to expanded use of popular sires. Koots and Crow (1989) reported little use of AI

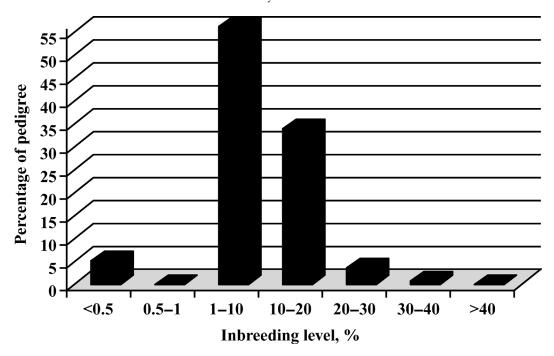


Figure 4. Distribution of inbreeding by level for individuals born between 1990 and 2001 (n = 1,656,153).

in Canadian Herefords in 1987, and it is expected that AI in U.S. Herefords was equally low.

Although the proportion of inbred animals is high in Herefords, the majority are lowly inbred (Figure 4). Of the animals born between 1990 and 2001, 62% had an F_x less than 10%. Almost three-fourths of these had an F_x less than 8%. In a review of cattle inbreeding studies, Burrow (1993) found that animals with inbreeding coefficients larger than 20% were more susceptible to inbreeding depression than those less inbred. In the current study, only 4.5% of the Herefords born during this period had an F_x greater than 20%. Individual sires or lines were not necessarily identified for this study, so the identities of animals with an F_x greater than 20% were not reported, but it is likely that many of these are descendants of, or currently exist in, one of the closed lines of Herefords being maintained.

Changes in Inbreeding

The prominent decrease in F_x from 1970 to 1980 warrants further examination to determine potential causes. Three different approaches were taken: 1) evaluation of genetic relationships between prominent sires and sire ancestry; 2) development and analysis of complete 12-generation pedigrees; and 3) simulating the effect of importing sires and dams.

Sire Relationships and Ancestry. Mean coefficients of relationship between the top 25 progeny-producing sires from 1950 to 2001 (Figure 5) were compared. Mean relationships from 1950 to 1969 generally were between 17 and 21%. Relationships decreased to a minimum of 10.2% in 1975, and remained between 10 and 15% through 2000. The decrease in mean relationship is

consistent with the decrease in mean inbreeding after 1969 and could indicate a gain in popularity of previously underrepresented lines or sires in the pedigree.

During the last half of the 20th century, breeders may have imported animals that would not have been in the association's pedigree file. The percentage of sires (from 1950) with unknown parentage and mean inbreeding for the full pedigree are shown in Figure 6. The percentage of sires with missing pedigree information was small and consistent until the early 1970s, when it increased rapidly through the early 1990s. The percentage of sires with missing pedigree information was small (1.3% at its peak), but assuming that most of the missing parentage is due to importation of genetics into the population, it is likely that the imported parents were widely selected for above-average performance. Although the proportion of progeny from these sires was less than 1% of all progeny (results not shown), the multiplicative effects of these genes on subsequent generations would likely affect the breed and may have contributed to the decrease in relationship between influential sires (Figure 5). The increase in unknown parentage coincided with the decreasing inbreeding trend and is one potential explanation for the decrease.

Complete 12-Generation Pedigrees. Figure 6 shows mean inbreeding using the subsample of animals born in 1990 to 2001 with at least 12 generations of pedigree to further investigate the impact of imported animals on inbreeding. The 12-generation inbreeding trend was relatively static until an increase in the 1980s. The annual inbreeding levels for the 12-generation pedigree did not have the distinctive dip in the 1970s and 1980s, as did the full pedigree. Importantly, the reduced data-

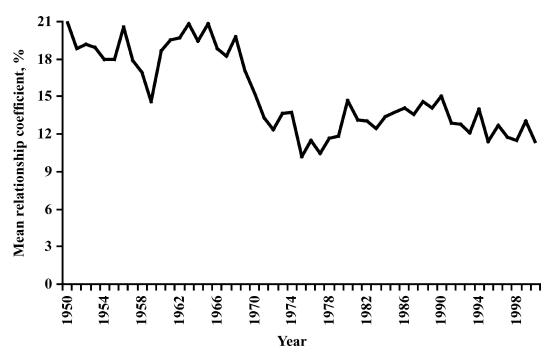


Figure 5. Mean coefficients of relationship between the 25 most-used sires each year from 1950 to 2000.

set shows how inbreeding, using a complete pedigree, increased to 18% by 2001. Almost one-third of animals born in 2001 had inbreeding levels exceeding 20%, compared with 6% of animals using the full pedigree (results not shown), indicating a high level of relatedness between animals in the 12-generation pedigree. These

results add a new dimension to the evaluation of inbreeding by illustrating how $F_{\bar{x}}$ increased for a subset of the population.

The comparison of the full and at least 12 generations of pedigree suggests that in this population, importation(s) decreased inbreeding for a period of time. Com-

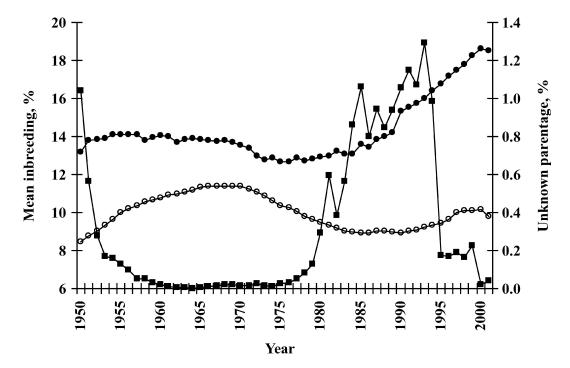
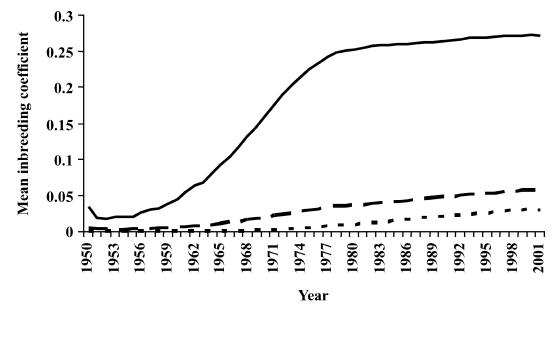


Figure 6. Mean inbreeding using the full pedigree (○), mean inbreeding using pedigrees of animals born 1990 to 2001 with all ancestors known for at least 12 generations (●), and percentage of sires used in each year with unknown parentage (■).



- - Rep0 = unaltered three-generation
- ----- Rep1 = all unknown parents replaced with one simulated sire
- Rep10 = all unknown parents replaced with one of 10 simulated sires

Figure 7. Mean inbreeding for a three-generation pedigree of animals born between 1990 and 2001 considering three simulation strategies.

parison of the percentage of highly inbred animals between the two pedigrees (33 vs. 6%) indicates that without outcrossing to imported animals, inbreeding would have been much increased. Although any importation was probably not directed at genetic diversity issues, it does underscore such actions as a potential avenue for introducing diversity.

Simulation. The conclusions above assume that progeny of imported animals and animals with unknown parentage are not related and thus the next generation is not inbred. This assumption may be valid in some cases but may underestimate inbreeding. To explore this aspect further, Figure 7 illustrates the change in mean inbreeding over time for the three scenarios: REP0, REP1, and REP10. Mean inbreeding for REP0, REP1, and REP10 from 1990 to 2001 was approximately 2.6, 27.0, and 5.2%, respectively. The REP0 inbreeding level of 2.6% represents a minimal level. The worst-case level of inbreeding would occur if all individuals with unknown parentage were related through just one set of parents (REP1). When individuals are related through multiple parent sets (REP10), the inbreeding increase is not as dramatic. The REP1 scenario is extreme, but it illustrates how inbreeding would have been driven upward if such a limited importation were made. The true value is likely to be intermediate between REP0 and REP10. A one-time importation of completely unrelated individuals would decrease inbreeding in their immediate offspring, but inbreeding would increase again when related animals were used as parents.

Annual Change in Inbreeding and Effective Population Size

The annual change in mean inbreeding $(\Delta F_{\bar{x}})$ was estimated for Herefords born during five time periods from 1946 to 2001, when inbreeding was changing at different linear rates (Table 3). The $(\Delta F_{\bar{x}})$ for the most recent generation is pertinent for studying the current and future genetic diversity of Hereford cattle, but comparisons to previous generations were used as a point of reference. The estimate of $\Delta F_{\bar{x}}$ for 1990 to 2001 was 0.12%/yr (Table 3), intermediate to the 0.09 and 0.22% levels reported by Ozkutuk and Bicard (1977) for English Herefords and MacNeil et al. (1992) for an inbred

Table 3. Annual change in mean inbreeding $(\Delta F_{\bar{x}})$ for five time periods

Years	$\% \ \Delta F_{x}$
1946 to 1966	0.13 ^a
1967 to 1969	$0.0^{ m b}$
1970 to 1979	-0.19^{c}
1980 to 1989	-0.031^{d}
1990 to 2001	$0.12^{\rm e}$

 $^{\rm a,b,c,d,e} Coefficients$ without a common subscript letter differ (comparison-wise), P < 0.001.

line of Herefords, respectively. The rate of inbreeding for 1990 to 2001 was linear and smaller than the $\Delta F_{\bar{x}}$ estimated for 1946 to 1966, indicating a slower accumulation of inbreeding during the 1990s than that which led to the maximum inbreeding in 1966. The annual change in inbreeding for each time period (Table 3) was smaller than the rate of 0.5% suggested by Nicholas (1989) as acceptable. The rates also were smaller than the 1% change per generation that Bijma et al. (2002) suggested was maximal for allowing continued genetic gain. Relative to some dairy breeds (Wiggins et al., 1995), the increase in inbreeding for Herefords is slower (linear vs. exponential increase), indicating breeders have opportunities to plan matings that will prevent inbreeding from becoming a production and genetic diversity issue.

The mean generation interval for the parents of animals born between 1990 and 2001 was 4.88 yr (results not shown). Using this figure and $\Delta F_{\bar{x}}$, an effective population size (N_e) of 85 was estimated for the 1990 to 2001 Hereford pedigree subset. The completeness of the pedigree (particularly for animals born 1990 to 2001) would suggest that $N_{e}\ was\ not\ overestimated$ (Boichard et al., 1997). This estimate of N_e is midranged compared with other cattle populations, where estimates have ranged from 21 to 257 for several European breeds of cattle (Kantanen et al., 1999; Gutierrez et al., 2003), 14 to 52 in Japanese Black cattle (Nomura et al., 2001), and 30 to 161 in U.S. dairy cattle (Weigel, 2001). In a breeding system designed to avoid close matings, Williams et al. (1988) found very small rates of inbreeding in two lines of Senepol cattle resulting in a N_e that was greater than 200. The N_e of 85 is larger than some that have been reported, but it is less than the 100 suggested by Nicholas (1989). Meuwissen and Woolliams (1994) reported critical effective population sizes for maintaining fitness ranging from 25 to 255. Meuwissen (1999) suggested that N_e below 100 animals is when population fitness decreases, and the United Nations Food and Agricultural Organization (2004) recommended that an effective size of at least 50 animals be maintained. The current level of N_e suggests that genetic diversity in Herefords is approaching critical levels, and if $\Delta F_{\bar{x}}$ were to increase, more aggressive actions would need to be taken if genetic variation were to be maintained.

Conclusions

This analysis provides a historical perspective and current benchmark of genetic diversity present in the U.S. Hereford population. As is expected in a relatively closed population, inbreeding increased over time. Such measurements are critical when evaluating genetic diversity and genetic conservation strategies. Our analysis showed that although the average inbreeding level for the breed is higher than other literature values for beef and dairy breeds of cattle, the rate of change was slower than values reported for dairy cattle. Due to the

slow rate of accumulation of inbreeding, breeders can limit its further increase without extraordinary measures.

The decrease in inbreeding during the 1970s was of particular interest in the study. The additional analysis performed demonstrated that the decrease could have been due to two separate breeder actions: 1) a shift in the lines used (as reflected in the decrease in genetic relationship between the most heavily used bulls), and 2) outcrossing to imported breeding stock that, from the American Hereford Association's records, had unknown parentage. Although both of these factors may have caused the decrease in average inbreeding, this effect was transient, as inbreeding started increasing again in the 1990s. The analysis that evaluated animals with at least 12 generation pedigrees also was instructive, as it provided an upper limit of inbreeding levels.

The work by Blott et al. (1998) demonstrated how Canadian and U.K. Herefords have become more related. It is likely that many of the Hereford imports that may have lowered inbreeding levels also were from Canada, implying a decrease in genetic diversity on a global scale. Such issues as presented above in conjunction with a 50% decrease in the number of annual registrations and the 60% decrease in the number of breeders may have significant effects on future inbreeding accumulation and the loss of diversity. In conjunction with such demographic changes, increased use of technologies (e.g., AI and marker-assisted selection) could rapidly reduce the breed's genetic diversity. As a result of these factors, breeders should monitor inbreeding levels to avoid potential decreases in productivity, as well as to preserve their options to alter the genetic composition of their cattle to meet future demands.

Implications

Inbreeding in the U.S. Hereford cattle population has increased at a linear rate from 1990 to 2001, but it remains below suggested critical levels. More than 95% of individuals are inbred but most at low levels. The effective population size of 85 in the latest generation suggests some decrease in genetic diversity. Maintenance of current genetic diversity for future generations should be addressed by developing mating strategies designed to minimize inbreeding.

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